

ANNALS
OF
The Entomological Society of America

Volume II

JUNE, 1909

Number 2

INVESTIGATIONS OF TOXOPTERA GRAMINUM AND ITS
PARASITES.

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This minute insect (see figs. 1, 2), aside from its economic importance, which, by the way, is very great, has become the basis of a long series of thorough investigations, carried out by several assistants of the Bureau of Entomology, under my direction. My own studies of the species were made largely during the years 1884 to 1890, while employed by the old Division of Entomology. As the subject of this paper may not be familiar to all entomologists it will be better to begin, historically at least, with our first knowledge of the species in its native country, if, indeed, we might with our present information, be allowed to designate for it a place of nativity.

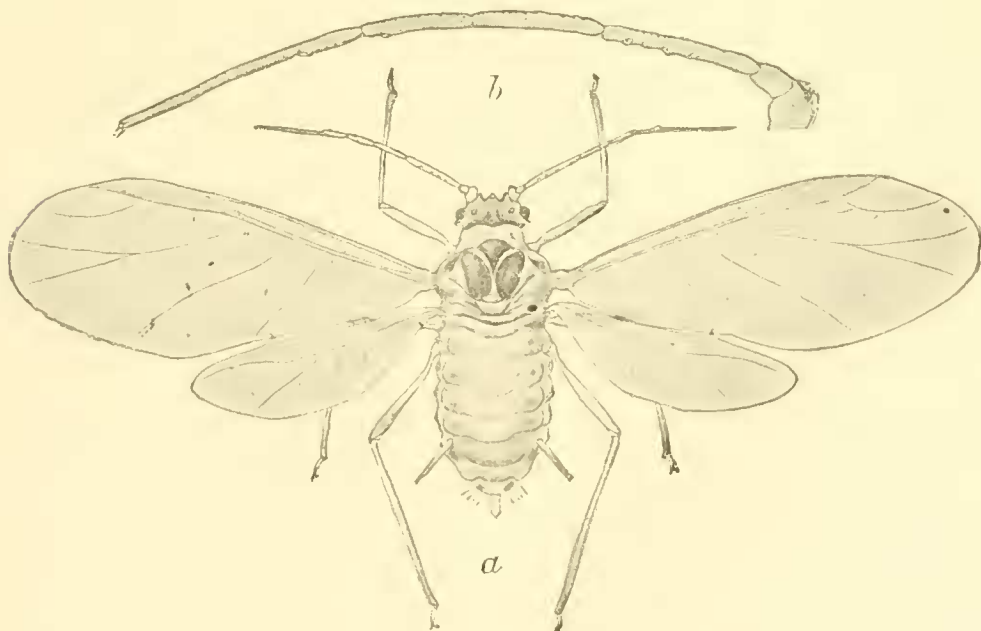


FIG. 1.—The spring grain-aphis (*Toxoptera graminum*): *a*, Winged migrant viviparous female; *b*, antenna of same. *a*, Much enlarged; *b*, highly magnified. (From Pergande.)

OCCURRENCE IN THE EASTERN HEMISPHERE.

It seems to have been observed at Parma, Italy, as early as 1847 (1). Five years later, in 1852, (1) Rondani, who described the species during this year, wrote to Professor Bertoloni under date of June 14, also from Parma, relative to the insect as follows:

"We have in our city an innumerable number of insects of a species of the *Aphis* genus, of Linnæus, of the order of Hemiptera.

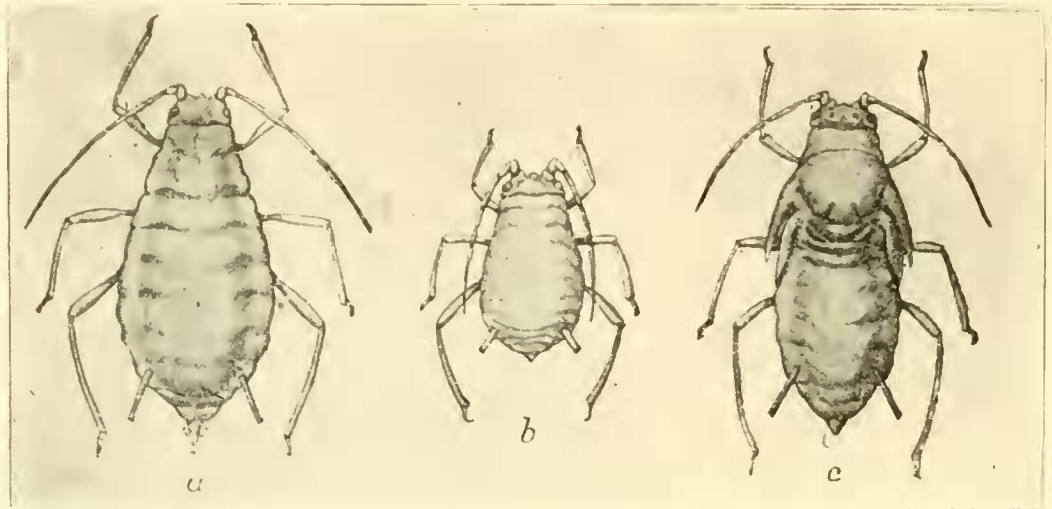


FIG. 2—The spring grain-aphis or "green-bug" (*Toxoptera graminum*: a, wingless female; b, larva; c, pupa. Much enlarged (from Pergande.)

Sometimes and in certain places the number of these insects flying in clouds in the air has been so great as to render them troublesome to people, entering the nose, eyes, and even the mouth when one cannot think how to protect oneself from them."

Elsewhere in this letter Rondani states that he had never been able to find it on any but graminaceous plants, where it nestled on the leaves. In commenting on this letter of Rondani, (1) Prof. Bertoloni takes occasion to say that:

"Innumerable specimens of the *Aphis graminum* Rondani, are seen in the streets of the city of Bologna and these have several times entered my nose and eyes when passing rapidly along the canal of Reno."

Passerini (2) excepted we find no mention of the insect again until 1884, when Dr. G. Horvath (3) mentions an attack on oats in Central Hungary in June, 1883. Ten years later, in 1894, Professor Karl Sajo, (4) records another outbreak, also in Hungary, again among growing oats.

Schouteden (5) in 1906, records the species from Belgium, but gives no further data except that it affects the graminaceæ.

In August, 1907, at the meeting of the International Society of Zoologists in Boston, and, later, also in Washington, I had the good fortune to meet Dr. Horvath and from him learned that the species had been found in Siberia on graminaceæ.

For two or three years past, grain in the Orange River Colony, South Africa, has been seriously affected by a species of *Aphis*, we having received several complaints of these invasions from Mr. H. Neethling, at that time, Chief of the Horticultural and Biological Division of the Department of Agriculture at Bloemfontein. It was only within the last few months, however, that we were able to secure specimens of these aphids for identification and, surprisingly enough, they prove to be *Toxoptera graminum*. With these were a number of individuals of a species of *Lysiphlebus*, allied to the one that is so efficient in holding the pest in check in America. This gives us records of the occurrence of the species in Europe, Asia and Africa.

OCURRENCE IN THE WESTERN HEMISPHERE.

The earliest information we have of the occurrence of *Toxoptera graminum* in America is in the year 1882, when it was received at the Department of Agriculture, but sad to say there is no record as to where the specimens came from. Late in June, 1884, it was found sparingly on wheat in the vicinity of Cabin John, a short distance north of Washington, and, about the same time, I found it infesting wheat plants in some breeding cages where some experiments were being carried on by myself at Oxford, Indiana, about one hundred miles southeast of Chicago, Illinois. Nothing more was heard of the species until 1890 when a very serious and destructive outbreak occurred in the West, extending from northern Texas to Missouri and central Indiana. Curiously enough there was little complaint from the territory east of the Appalachian mountain system, even where considerable wheat and oats were being at that time grown. Again, we have a period of eleven years without noticeable injuries from this pest; then, in 1901, there came the most destructive outbreak that had occurred up to that time, but in this instance depredations did not extend farther north than central Oklahoma, though planters in South Carolina afterwards reported "green lice" as having been very abundant on oats during the spring of that year.

In March, 1903, there was an incipient outbreak of the species in northern Texas. But this seems not to have extended northward beyond the Red River and was overcome by parasites in

April. (6) This time it certainly did appear in excessive abundance on fall-sown oats in North and South Carolina, and planters became alarmed over its presence. It did not, however, work serious injury there.

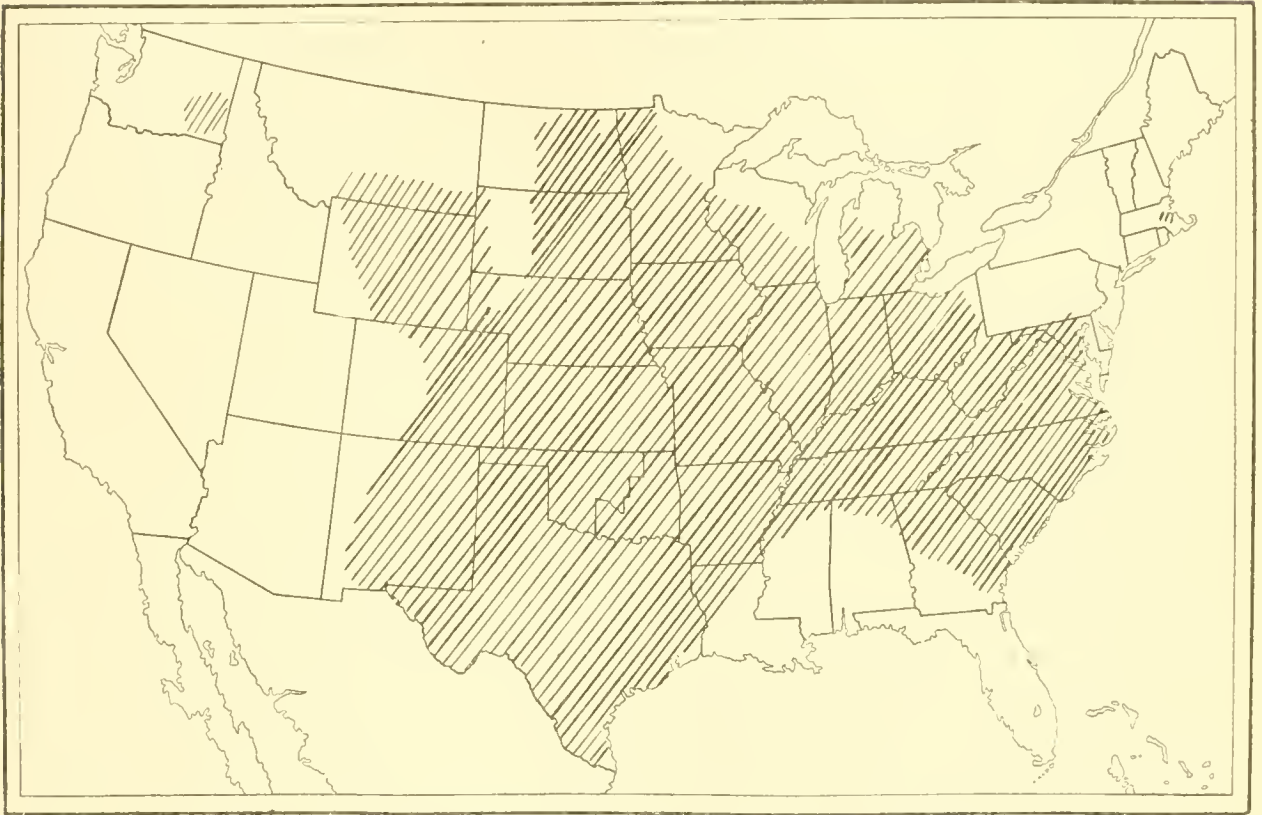
In December, 1906, the insect began to appear in fields of fall sown and volunteer oats in northeastern Texas. Throughout the winter of 1906-1907 they increased in abundance and by spring had ravaged the fields of both wheat and oats throughout Texas and Oklahoma, east of the 100° meridian, and as far north as Wichita, Kansas, but spring sown oats were damaged as far north as eastern Iowa, northern Illinois and southern Wisconsin. In the east there was also serious damage to wheat and oats in both of the Carolinas. The loss by reason of this outbreak would probably not fall short of \$12,000,000 to \$15,000,000 and proved to be much more serious than any preceding occurrence. Thus it will be observed that the species is becoming constantly more abundant, its re-occurrences more frequent and more threatening to grain crops, especially throughout the country between the Rio Grande and Missouri rivers. This is also true to a less degree in the Carolinas.

DISTRIBUTION IN AMERICA.

Most rigid searches have failed to reveal the presence of the insect in the country between the St. Lawrence river, Lake Ontario and Lake Erie, and the coast, to a line drawn from Cleveland, Ohio, to Philadelphia, Pa., although it would not be surprising if it extended farther northeast nearer the sea coast.* Neither has it been found in northern Michigan, northern Wisconsin, northeastern Minnesota, or in the arid region of western North and South Dakota or eastern Montana, where it has also been diligently searched for. It has not been found in Alabama, Mississippi, or Florida, but has not been searched for in those States. With these exceptions it ravages over the whole country east of the Rocky Mountains, from Mexico northward into Manitoba and Saskatchewan, and from an elevation little above sea level, to 8,000 feet in New Mexico. On the Pacific slope it is found in eastern Washington. Whether it also extends from Washington southward along the Pacific coast to Mexico is not known, because it has not been searched for in that portion of the country. (See map.)

* Mr. Paul Hayhurst, assistant to Dr. Wheeler, states that he has found it on oats, *Agropyron repens* and *Dactylis glomerata*, in the vicinity of Forest Hills, near Boston, Mass.

If we assume that Southern Europe is the original home of the species, its occurrence in the western hemisphere can only be accounted for on the score of introduction, but the distribution of the species in the eastern United States, does not in the least indicate such an introduction as having come through any of the Atlantic coast seaports. On the other hand, its occurrence all along the Rio Grande River bordering Mexico, together with its destructive abundance in northern Texas, as early as 1890, only



DISTRIBUTION OF TOXOPTERA GRAMINUM IN THE UNITED STATES.

eight years after its first discovery in America, goes far to strengthen the theory of an early introduction into some country to the South, and a natural diffusion over the United States, following the same lines of dispersion as for so many other species coming to us from Mexico and southward.

FOOD PLANT.

The species is essentially a leaf infesting insect, rarely infesting the stem. While preferring oats it will readily attack wheat, rye, barley, and may often be found on the underside of the lower leaves of corn. Corn excepted, its effect on the foliage of grain, when present in large numbers, is to cause the infested leaves to change to a red color, which seems to be very characteristic of *Toxoptera* and does not follow, to a marked degree, attacks of

other species of Aphids on these grains. The insect also has been found breeding upon a considerable number of native grasses any one of which may constitute its alternating food plant, upon which it may survive the summer in different portions of the United States. It has been found breeding freely upon *Alopecurus geniculatus* in Oklahoma by Mr. W. J. Phillips and by Mr. C. N. Ainslie in Kansas; on *Agropyron occidentalis*, also in Oklahoma, by Mr. Phillips; and by Mr. O. E. G. Kelly and Professor Gillette in Colorado. *Agropyron tenerum* was found moderately infested by Mr. C. N. Ainslie at Las Vegas, New Mexico. It was found breeding upon *Bromus* at Washington, D. C., and also upon *Bromus porteri* at Las Vegas, New Mexico, and on an undetermined species of *Bromus* at Mesilla Park, New Mexico, also by Mr. Ainslie. I observed it very abundantly on *Dactylis glomerata* in Indiana in 1890, and again excessively abundant in a small, isolated meadow, of this grass near Midlothian, Virginia, in April, 1907. This meadow was located in a region not adapted to the growing of grain and there was no field of growing wheat or oats within five miles. Mr. Kelly found it inhabiting *Distichlis spicata* in such abundance as to be damaging this grass in Montana, which in that part of the country is known commonly as "salt grass." It was found inhabiting *Elymus striatus* at Las Vegas, New Mexico by Mr. C. N. Ainslie. Mr. W. J. Phillips found it attacking *Hordeum pusillum* at Beloit, Kansas, and, Kingfisher, Oklahoma, while I found this to be of frequent occurrence throughout Kansas. Mr. Kelly observed it abundant on *Hordeum jubatum* in Montana, while Mr. C. N. Ainslie found it moderately abundant on *Hordeum cæspitosum* near Cimarron, New Mexico. Wherever *Poa pratensis* grows the insect will probably be found breeding upon it through the entire summer. In fact this has been actually observed to occur in the city of Washington. Mr. Phillips has also observed it in Indiana and throughout the northern sections of the country, where *Toxoptera* occurs; it is more likely to be found on this plant during summer than upon grain, excepting, perhaps, during seasons of excessive abundance. Mr. C. N. Ainslie also found it moderately abundant on *Polypogon monspeliensis* about Albuquerque, New Mexico. It has been found breeding on *Stipa viridula* at Las Vegas, New Mexico, by Mr. C. N. Ainslie, the grass being heavily infested. As one or more of these grasses will be found to occur in almost every portion of the United States, it would appear that the non-

occurrence of *Toxoptera* in any considerable section of the country cannot be due to a lack of uncultivated food plants. Mr. Phillips found that the species readily developed on the following plants in his breeding cages: *Dactylis glomerata*, *Eleusine indica*, *Eragrostis pilosa*, *E. megastachya*, *Sporobolus neglectus*, *Agropyron* sps., *Elymus virginicus*, *E. canadensis* and *Bromus secalinus*.

SEASONAL HISTORY.

Though in the main following quite closely the developmental habits of other Aphids, this species exhibits some striking contrasts. While it probably passes the winter in the egg state in the northern portions of the country, it is quite certain that it is not restricted to that mode of hibernation during mild winters, or in the South. The fact that viviparous ♀♀ (figs. 1, 2) sent from Leavenworth, Kansas to Washington, D. C., in March, and there placed indoors, produced oviparous ♀♀ (fig. 3) and ♂♂ (fig. 4) in April, and, in case of the latter, even till May 18, shows that the sexes may occur in spring. As information on the occurrence of the sexual forms appears to be entirely lacking in the South, it would be too much to connect the presence of these forms in spring as showing a changed summer condition in the South, whereby the dry season instead of the winter might be passed in the egg. Bearing upon this point, but proving nothing unfortunately, it may be stated that at Richmond, Indiana, in the autumn of 1907, Mr. Phillips encountered a pronounced lack of oviparous ♀♀, the weather being unusually wet. During a corresponding period of 1908, with one of the severest droughts on record prevailing at the time, he was unable to get a sufficient number of viviparous ♀♀ to keep up his experiments, while the sexual forms were present in abundance.

Two of my assistants, Mr. W. J. Phillips, and Mr. C. N. Ainslie, have on occasions dissected ♀♀ and found both eggs and embryos in the ovaries, the latter in spring; while the former, in the fall, observed in one instance that the eggs were in one side and the embryos in the other side of the abdomen, as though one ovary had produced eggs and the other embryos.

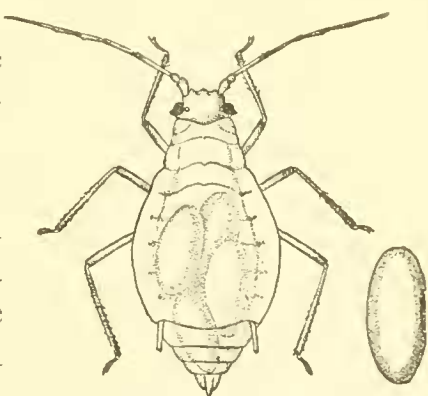


FIG. 3.—Spring grain-aphis (*Toxoptera graminum*): Oviparous female with eggs in body, greatly enlarged; at right, egg still more enlarged. (Original.)

Mr. Phillips in a long series of breeding experiments carried out at Richmond, Indiana, has found that the oviparous ♀ will not deposit eggs without having first mated with the ♂, and usually produces not more than five or six eggs. The life of the viviparous ♀ is much longer than that of the oviparous ♀ but the life of the latter is greatly prolonged if she fails to meet the ♂ and become fertilized.

HIBERNATION.

The species will breed at about or a little above 45° Fah., though, as determined by Mr. Phillips, they do not reach their maximum until the temperature rises to above 50° Fah., which, however, is still too low to render their parasites active. As an experiment, a miscellaneous lot of individuals were frozen up in ice

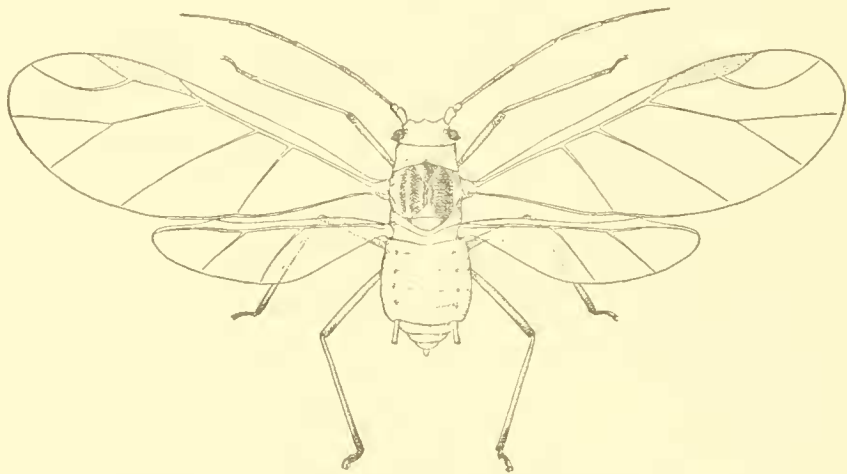


FIG. 4—Spring grain-aphis (*Toxoptera graminum*: Male. Greatly enlarged. (Original.)

for five, twelve and twenty-four hours respectively, and on being thawed out the older individuals all succumbed; in another twenty-four hours experiment, using individuals of different stages of development, only the pupæ of the viviparous ♀ survived. Viviparous ♀♀ brought indoors from a temperature of 11° Fah., and thawed out began to give birth to young in about three hours. Thus it is that the species is able to withstand the climate of northern latitudes and high altitudes. As it breeds freely in a temperature of 100° Fah., in the shade, presumably still higher in the open, on the public grounds in Washington, it would seem that farther south, where it was found by Mr. C. N. Ainslie, the insect would encounter even a greater degree of heat in summer. Thus we have a fairly good basis for the supposition that it

extends southward beyond the boundaries of the United States. So far we have not found the sexual forms south of southern Kansas, about latitude 37° , but north of this latitude it can certainly pass the winter ordinarily in the egg state and in mild winters as viviparous ♀♀ either wholly or in part developed. South of Lat. 37° there really seems to be no vital necessity for sexual ♀♀ in order to perpetuate the species or to enable it to pass the winter. Indeed, the greatest need would seem to be for some means of bridging over the dry period, during which there is a serious lack of food and in a temperature far too high to induce torpidity thus rendering food unnecessary.

DEVELOPMENT DURING SUMMER.

Beginning July 8, 1907, Mr. W. J. Phillips, at Richmond, Ind., began a study of the continuous generation of this species, following it through to December 10, besides securing sexual ♀♀ and eggs therefrom on blue-grass in the fields in October. With these eggs, he began March 27, 1908, to again follow out continuous generations, commencing with the first stem mother that hatched from eggs deposited the previous autumn. From the wintered over egg to the oviparous ♀, or from one egg stage to the other, the maximum was twenty-one generations of viviparous ♀♀ when the first born were used in each case, but only ten generations where the latest born was used in a parallel experiment. The experiment ended December 1, 1908. It is not unlikely that there are a greater number of generations produced in the south, where the warm period is more prolonged, though in the north this period while shorter is not usually so excessively dry.

Ordinarily, the viviparous ♀ will reach full development and herself begin reproduction about eight days from birth, but in late autumn this period becomes very irregular. In one case Mr. Phillips had a viviparous ♀ under observation, under outside conditions from the day of her birth October 18 to December 10. Though apparently fully developed she produced no young and went into winter in a most vigorous condition. It will be noted that it was just such as these that survived the freezing experiment previously described. The young, when born, are enveloped in a membraneous sack, from which they disengage themselves almost the instant they leave the mother. A viviparous ♀ may produce as many as 70 young scattering them throughout a period

of four to six weeks. The wingless viviparous ♀ ♀ are more prolific than the winged, but, of course, scatter their young less as they are confined to a very limited area. It is usual to observe a wingless mother stationed on a leaf in the midst of a family of a dozen or more young, varying in size from newly born to half grown. The insect moults four times.

EFFECT OF METEOROLOGICAL CONDITIONS.

As has already been shown, the direct effect of low temperature on the insect is, in the south at least, exceedingly small. It is vastly more probable that the influence of winds and humidity are much more important factors, though of the latter we cannot yet speak with the fullest assurance.

As has also been shown, it may turn out that hot dry weather may be found to greatly influence the time of appearance and abundance of the ♂ and sexual ♀.

Winds certainly do have considerable influence in the dispersion of the winged viviparous ♀ ♀, during the seasons of excessive abundance, and as it is well known that a diminution of the food supply, like the killing of the grain plants, tends to produce winged instead of wingless individuals, it will be seen at once that the occurrence of these winds at the time of a serious outbreak may become a powerful factor in the spread of the pest. Now, the prevailing winds in the Southwest during spring are from a southerly direction and as there is a continually increasing food supply to the northward as the season advances, these winds help the insects to keep pace with this advance. This diffusion might be likened to a horizontal revolving movement, the winged ♀ ♀ from a destroyed field passing over others along the border and settling down to breed, infest and destroy other fields more in advance, and so on day after day, thus passing over miles upon miles of young growing grain changing it from a luxuriant green to reddish brown, as effectually destroying it as would be the case were it to be scorched by fire. There are of course other modes of dispersion, and I have observed not only winged individuals but also parasites, clinging to the glass of the windows in railway coaches and in this way carried long distances.

Thus it is that an invasion of *Toxoptera*, originating in central northern Texas in a winter temperature above the normal, yet too cool to admit of its chief natural enemy becoming active, will

develop countless millions of winged viviparous ♀♀, and these will gradually become diffused northward as the season advances and weather conditions favor them. Indeed the experience of Rondani and Bertoloni, in Italy, found an equal in the southwest in 1907 where Mr. C. N. Ainslie observed the winged ♀♀ in such swarms as to interfere not only with a Sunday game of baseball, but also with the conducting of a funeral. North of about Lat. 38° the season is so far advanced that wheat becomes too large and tough to offer the requisite food supply, but spring oats here prove a convenient and attractive supplement and it is usually this crop that suffers most to the northward, provided, of course, the weather conditions are not favorable to the development of natural enemies.

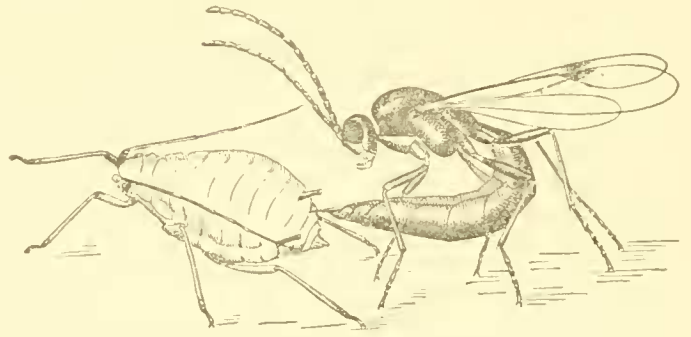
NATURAL ENEMIES.

There are a number of these, especially among the Coccinellidæ, several species of which feed, both in the larval and adult stages, on *Toxoptera*. Syrphus flies and Chrysopa also destroy them. *Aphelinus nigritus* Howard, recently described, is a minute parasite that has been reared from this insect in South Carolina by Geo. G. Ainslie, and in New Mexico by Chas. N. Ainslie, both assistants in the Bureau of Entomology. Quails are very fond of them and Miss Margaret Morse of Clarke University has been kind enough to make some experiments for us in feeding these birds. Miss Morse estimates that about 5,000 individual *Toxoptera* were eaten by a single quail in one day, preference being shown for those that were unparasitized. The Song Sparrow, *Melospiza melodia*, also devours great numbers of them in the grain fields.

DEVELOPMENT AND INFLUENCE OF *LYSIPHLEBUS TRITICI*.

As a matter of fact, however, all of the natural enemies previously mentioned are of small moment as compared to the influence of the one minute parasitic species *Lysiphlebus tritici* (figs. 5, 6.). It is this species, or what we are at present terming as such, that normally holds *Toxoptera* in check in this country, and so long as its development and activity are not obstructed by meteorological conditions, it will probably continue to do so. Indeed so important is this insect and so powerful is its influence that only a short space of from ten days to two weeks time is

required for it to overcome a most serious outbreak of *Toxoptera* and thus save from destruction vast areas of growing grain. The species winters over in the fields in the bodies of its host. In many cases this hibernation is passed as nearly or quite fully developed adults, ready to emerge when the temperature rises to the



neighborhood of 56° and continues for a sufficient length of time, and where they have been prevented from emerging the previous fall, on account of the advent of cold weather. This is clearly shown by the fact that Mr. E. O. G. Kelly found them in this condition at Leavenworth, Kansas, on November 13. From a lot of 50 parasitized *Toxoptera* that had been washed or rubbed off

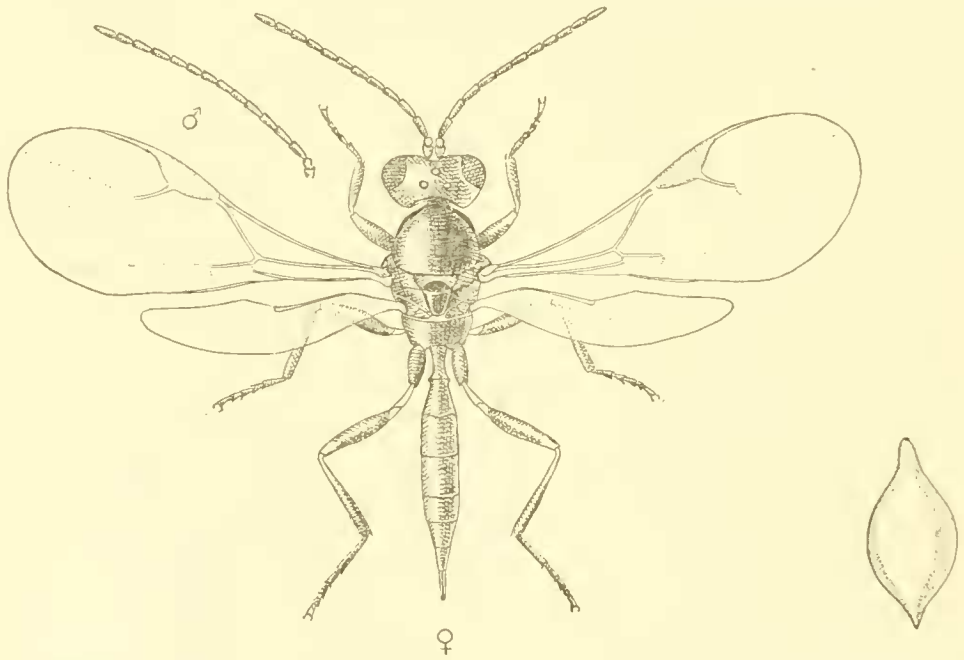


FIG. 6.—*Lysiphlebus tritici*, principal parasite of the spring grain-aphid; Adult female and antenna of male. Greatly enlarged (original). At right: Egg of *Lysiphlebus tritici*. Highly magnified (original).

the leaves of the young grain (fig. 7) and were taken out of the mud about the wheat plants on February 28, after the winter was practically over, Mr. Kelly found that of these 50 dead bodies, 17 contained full grown larvæ of the parasite, 12 contained pupæ of a light color and 21 contained pupæ of a dark color, the latter

evidently ready to promptly develop with the advent of warm weather. Mr. Kelly, on the same date, also secured a large number of *Toxoptera* in various states of development that were hibernating in wheat fields near Leavenworth, Kansas. The weather had been such as to preclude the possibility of these having been recently parasitized. Yet some of them soon began to show the characteristic yellow color of a *Toxoptera* parasitized by *Lysiphlebus*, and adults were afterwards reared from them. This shows conclusively that *Lysiphlebus* hibernates in advance stages of development in the bodies of its host, which they have killed the previous autumn, as well as larvæ in hosts wintering over from half to fully grown.

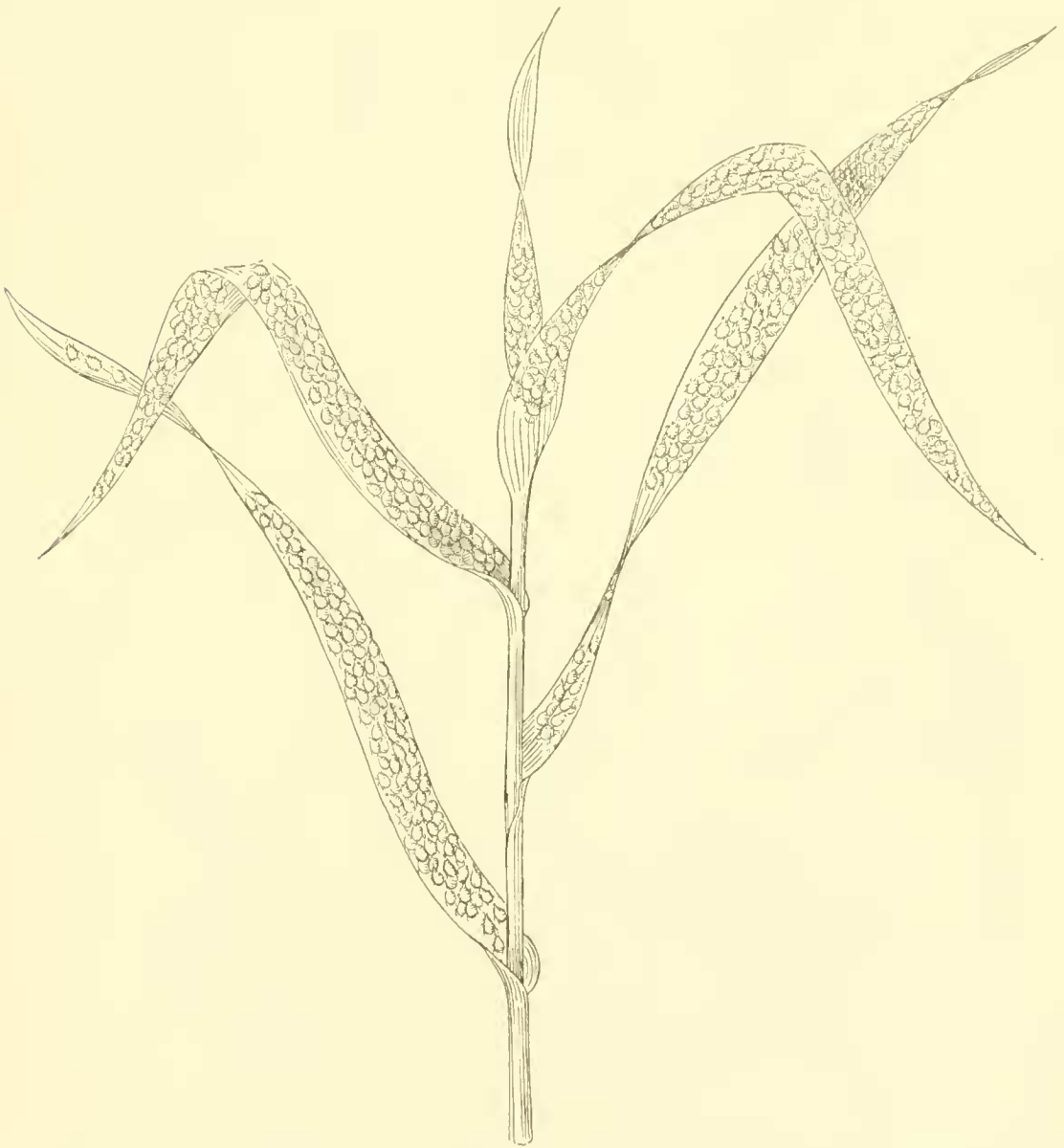


FIG. 7.—Stalk of wheat, the leaves covered with dead spring grain-aphids killed by the parasite *Lysiphlebus tritici*. About natural size (original).

The ♀ *Lysiphlebus* is even more prolific than *Toxoptera*. Mr. Phillips has found ♀ ♀ with upwards of 400 eggs in their ovaries, and Mr. Kelly has reared in some cases 206 individuals from a single mother *Lysiphlebus*. The eggs are lemon shaped and white in color. When excessively abundant the parasite will thrust its ovipositor into old and young aphids of both sexes, including the sexual ♀, even though previously parasitized; and Mr. Phillips has observed them to apparently oviposit in the dead bodies of those that had been killed by fungus attack. When their numbers are not so great, they show more discrimination and seem to prefer half grown individuals in whose bodies to place their eggs.

This species of *Lysiphlebus* is parthenogenetic, as was first observed by Mr. Phillips at Richmond, Indiana, and afterwards more fully elucidated by Messrs. Kelly and Urbahns at Wellington, Kansas. The experimental breedings of Mr. Phillips in 1907 indicated that the offspring of virgin ♀ *Lysiphlebus* were always exclusively ♂ ♂. In a series of upwards of eighty breeding experiments carried on indoors, in 1908, by Kelly and Urbahns, only forty-eight gave results of any kind. Of these only four gave ♀ ♀, the other giving only ♂ ♂. In the four exceptional cases the ♀ ♀ kept virgin, ran all to ♂ ♂, two with the first generation, one with the second and one with the third. The mode of procedure was as follows:

Starting with a mated ♀, the ♀ ♀ from among her offspring were isolated, even before emergence; on their appearance these were given *Toxoptera* reared under cover to preclude parasitism; the few ♀ ♀ from among this second generation were again isolated in the same manner, the ♀ ♀ in all cases being kept unmated. It was thus found possible to breed a limited number of ♀ ♀ parthenogenetically to and including the third generation. Beyond this all offspring were ♂ ♂, this seemingly being the limit. Just why such a large percentage of these experiments should have proven abortive is not clear. The conditions under which they were carried out were of course unnatural but much more protected from the adverse elements of the open field.

The egg of the *Lysiphlebus* normally develops to the emerging adult in about ten days, during the first six of which the host insect remains alive, and at the end of that period commences to take on a yellowish hue, the larvae of the parasite showing clearly through the skin of the abdomen (fig. 8).

Some studies were made of the final larval stage by Miss Weeks, of Manhattan, Kansas, under my supervision, the results of which were given in brief by me at the first meeting of this Society in Boston, and are as follows:*

A wingless ♀ of *T. graminum* was taken from the field when beginning to take on the yellowish color, which first denotes parasitism, and which precedes the amber color of the more advanced stage. Evidently this was on or about the sixth day from the time of oviposition by the *Lysiphlebus*, the larva being at the time quite full grown and occupying its normal position in the posterior part of the abdomen of the host insect. From all that we have been able to learn the very young parasite larva takes this position, and, refraining from moving about to any considerable degree, it does not come in contact with or injure any vital organ of its host, the effect being to reduce the period of reproduction of the ♀ *Toxoptera* to a very few days at most. But on reaching its full larval development, it seems suddenly to become more active, and with its first extended travels within the abdomen of its victim the last spark of life remaining in the latter is extinguished. It was just at this point that the observations herein recorded were made.

On bringing the ♀ *Toxoptera* from the field and placing it under the microscope, the *Lysiphlebus* larva was observed to work its way actively about as shown by the accompanying plate, these movements being always forward and easily observed through the skin of the victim until this had become too opaque. The movements of the parasite larva were accompanied, on the part of the victim, by a clutching of the leaf and a rigidity of the muscles of the limbs. But it has since been learned that this *rigor mortis* has little if anything to do with the adherence of the cocoon to the leaf surface, as was previously supposed by me, except perhaps to temporarily hold the body of the aphid fast until the parasite larva can anchor it more securely. (See Proc. Ent. Soc.

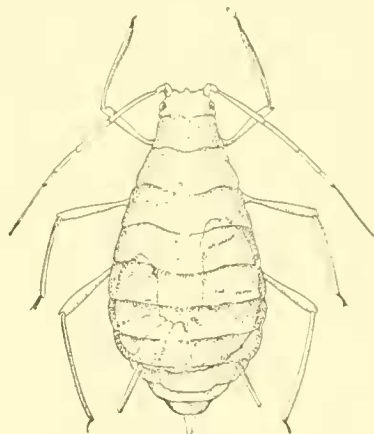
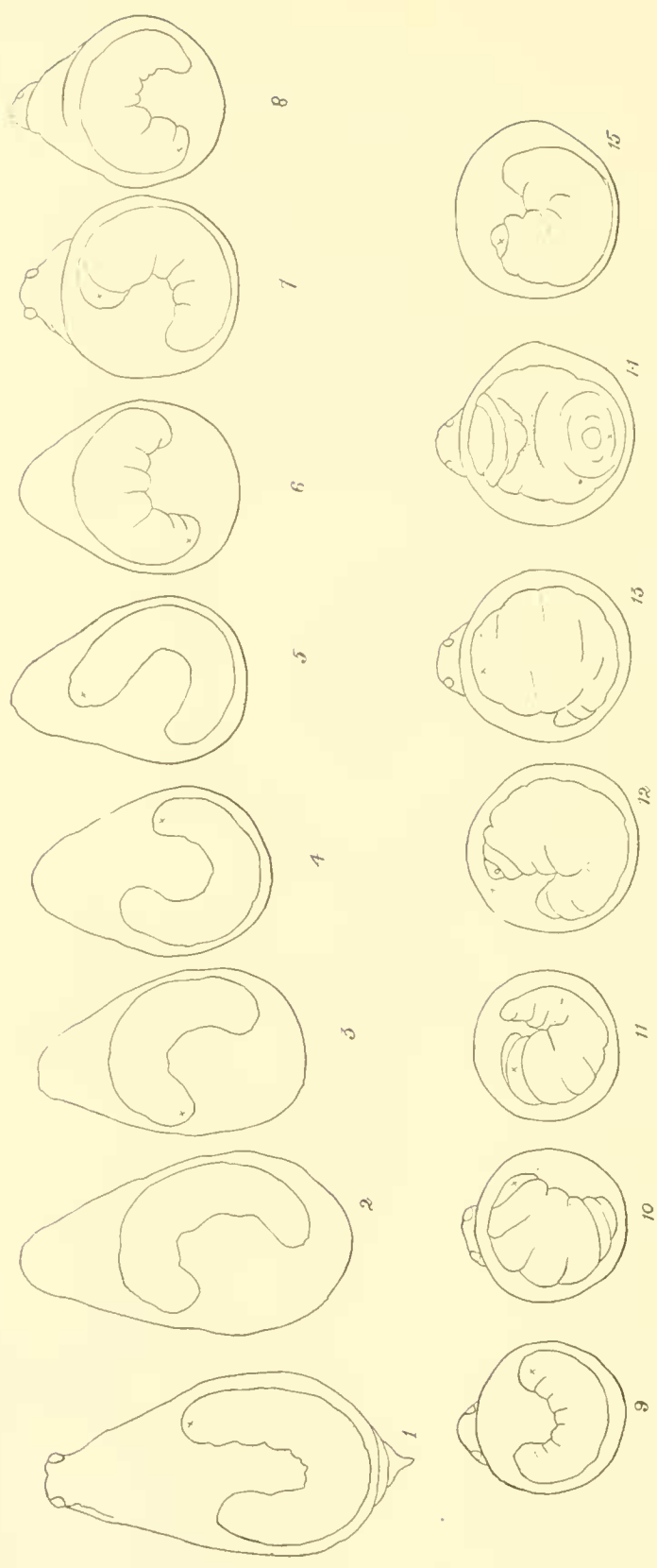


FIG. 8—Wingless female of spring grain-aphis, containing larva of the parasite *Lysiphlebus tritici*. Much enlarged (original).

* These observations were afterwards published in Proc. Ent. Soc. Wash., Vol. IX, Nos. 1-4, pp. 110-113, Plate VI.



THE FASHIONING OF THE PUPAL ENVELOPE IN *LYSIPHLEBUS TRITICI* ASHM.

F. M. Webster.

Wash., Vol. IX, p. 111.) Later observations by Mr. Kelly on the movement of the parasitic larva, made from beneath and after the dorsal skin of the host had become too opaque to continue them from above, shows that the ventral skin of the *Toxoptera* splits and the slit thus formed widens, as the skin assumes a rotund shape, until it becomes nearly circular. The parasite larva spins a cocoon of silken threads within the empty skin of its host, and, by reason of this disc-like hole in the ventral surface of the host skin, attaches the whole structure firmly to the surface of the leaf.

Taking up these observations in detail, figure 1 of plate XIV shows the host as when first placed under the microscope at 11 A. M., while she was still alive and at a time when she seemed to tighten her grasp on the leaf with each movement of the parasite larva within her body. Between 11 A. M. and 11:35 A. M. the *Lysiphlebus* larva had made three complete revolutions in the body of its host, some of the different positions assumed, as also the gradual shaping of the skin of the now dead *Toxoptera* being illustrated by figs. 2-7 in the plate. Between 11:35 and 11:40 A. M., the larva had completed another revolution, probably the fourth from the beginning. The fifth revolution was completed by 11:30 A. M., and the sixth at 11:58 A. M., while the seventh was completed by 12:07 P. M. With the eighth revolution, shown by figs. 8 and 9, completed at 12:11 P. M., the skin of the host insect had been brought into its rotund shape and the larva had just begun to contract preparatory to pupation. At 12:15 the ninth

EXPLANATION OF PLATE XIV.

FIG. 1.—Position of larva of *Lysiphlebus tritici* in body of wingless adult ♀ of *Toxoptera graminum*, just before beginning its revolutions for fashioning the body of the *Toxoptera* into a pupal envelope, 11 A. M.

FIGS. 2-7.—Some of the positions assumed by the *Lysiphlebus* larva between 11 A. M. and 11:35 A. M., during which time it made three complete revolutions.

FIGS. 8, 9.—Positions during and at completion of eighth revolution, 12:11 P. M.

FIG. 10.—Position at completion of ninth revolution, showing contraction of the larva, 12:15 P. M.

FIG. 11.—Position at 12:20 P. M.

FIG. 12.—Position at 12:22 P. M.

FIG. 13.—Position at 12:27 P. M.

FIG. 14.—Position at 12:32 P. M.

FIG. 15.—Position at 12:32½ P. M.

rotation (fig. 10) had been completed and the larva had decidedly contracted. Fig. 11 shows the situation of both larva and pupal envelope at 12:20; fig. 12, at 12:22; fig. 13, at 12:27; fig. 14, at 12:32, and fig. 15, at 12:32½ P. M. At 12:35 P. M. there were apparent on the body of the parasite larva small, roundish cells of a yellow color. By this time the skin of the host had reached the semiglobular, typical form, which did not materially change afterward, though a slight movement in the larva could be detected up to 4 P. M., after which the covering had become too opaque to permit of further observations. Thus, within the space of five hours the living body of the host had been transformed into a tough, dried, hardened protective covering the cocoon of the parasite during its short pupal stage, by a process of manipulation by the larva and a natural tanning process which renders the skin of the dead *Toxoptera* so impervious to the weather that these skins so prepared, may be washed off the leaves by beating storms, yet do not become easily disintegrated, and may often be found in quantities on the ground underneath the infested grain plants.*

While the normal position of the larva of the parasite in the abdomen of the host is indicated in Plate 1, fig. 1, there are exceptions, as shown by a case where, in a very young *Toxoptera*, the position illustrated in text fig. 9 was assumed. This, however, is unusual. Again, while the transformation of *Lysiphlebus* from egg to adult takes place within the pupal envelope, as previously described, and the adult makes its way out by way of a small disc which it gnaws through both cocoon and skin and pushes outward, as shown in fig. 10. Yet, sometimes, the larva works out of this case prematurely, as shown in text fig. 11. This may, perhaps, be due to some mishaps in constructing the anchorage previously mentioned. Mr. C. N. Ainslie found several of these prematurely issued larvæ on the ground in wheat fields in Kansas, under very seriously infested grain plants where the *Toxoptera* were very much parasitized.

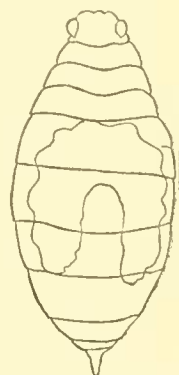


FIG. 9 - Unusual position of larva of *Lysiphlebus tritici* in body of *Toxoptera graminum*. Enlarged (original).

* NOTE: Mr. Kelly has since found that the parasite slits the ventral skin of the host, and, widening the rent spins a cocoon within the aphid skin and anchors it fast where the slits are situated.

The celerity with which an invasion of *Toxoptera* is overcome by *Lysiphlebus*, is frequently a matter of wonder, as it hardly seems possible that this host alone could be the source of the swarms of individuals that make their appearance after a few warm days have elapsed, in the midst of an unseasonably cool spring, preceded by a winter abnormally mild.

In order to determine the origin of these myriads of parasites, Messrs. Kelly and Urbahns began a long series of experiments at Wellington, Kansas, to determine whether there might not be a multiplicity of host species from which great numbers of *Lysiphlebus* would emanate to fall upon and destroy *Toxoptera* whenever it becomes excessively abundant. The entire failure to introduce these parasites in advance of an invasion of this character from the south, as was the case in Kansas in May, 1907, has indicated that such introductions were not possible and that to attempt it was a veritable carrying of coal to Newcastle.

Female *Lysiphlebus* from *Aphis brassicæ* taken from the field were first bred into *Toxoptera* from which adults were obtained.

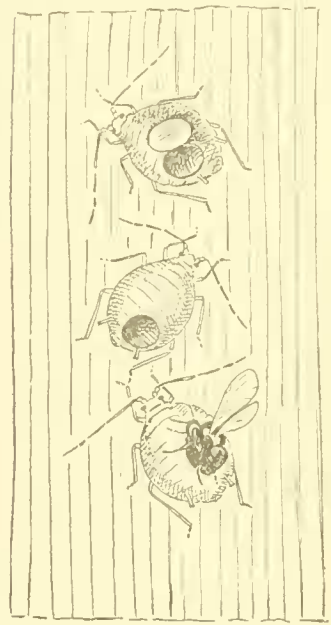


FIG. 10—Dead "green bugs," showing hole from which the matured parasite of *Lysiphlebus tritici* emerges. The top figure shows the lid still attached, but pushed back; the bottom figure shown the parasite emerging. Enlarged (original.)

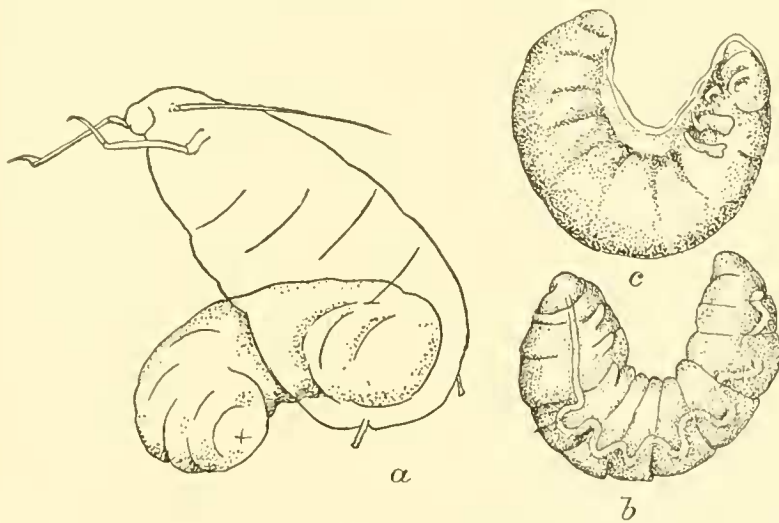


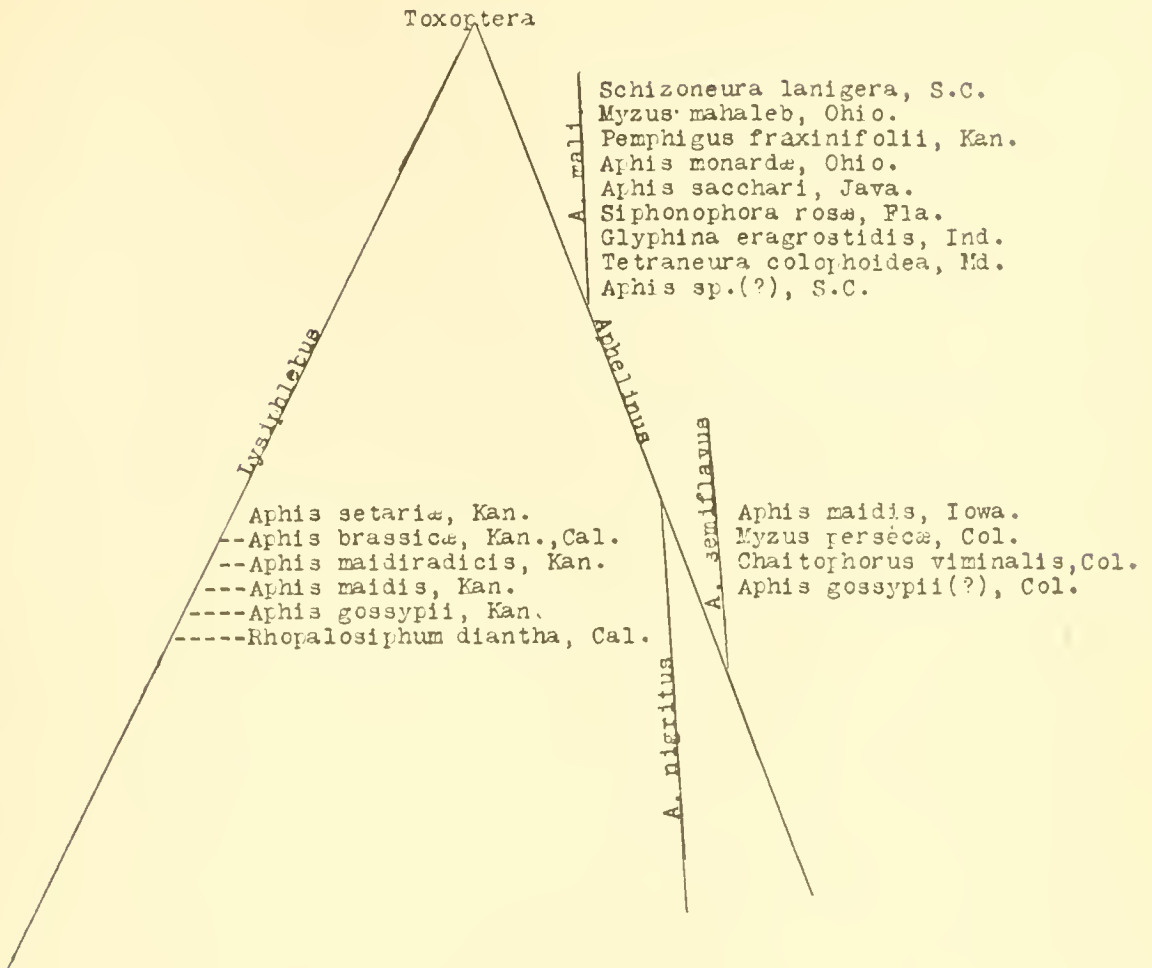
FIG. 11—*a*, Larva of *Lysiphlebus tritici* working its way prematurely from body of *Toxoptera graminum*; *b*, same larva, somewhat further developed; *c*, same, still more developed. Enlarged (original).

This experiment was several times repeated. Female *Lysiphlebus* reared under cover from *Aphis maidiradicis* were in two cases bred into *Toxoptera* and adults obtained. Female *Lysiphlebus* were reared from *Aphis setariæ* from the field and the issuing parasites in two cases were bred into *Toxoptera* and adults secured. This was also repeated several times. Female *Lysiphlebus* reared from *Aphis maidis* from the field, the adult parasites were bred into *Toxoptera* and adults emerged. Repeated several times. Female *Lysiphlebus* from *Aphis gossypii* from New Mexico and the adults successfully bred into *Toxoptera*. Female *Lysiphlebus* reared from *Aphis setariæ* from the field were bred into *Toxoptera* thence into *A. maidiradicis* and back into *Toxoptera*. Female *Lysiphlebus* from *A. setariæ* taken from the field and bred into *Toxoptera*, then back into *A. setariæ* again into *Toxoptera* and then into *A. brassicæ* from which adults were secured.

In many cases these breedings were reversed. The only cases of failures were in attempting to breed *Lysiphlebus* from *Toxoptera* into *Chaitophorus*; and in attempting to breed *Lysiphlebus* from *Toxoptera* into *Macrosiphum rudbeckiæ*. These experiments were reversed with the same results.

These experiments will be carried further another year, as it seems that host habits if we may term them such may possibly divide the specific position of the parasite in future.

The following diagram will serve to illustrate the additional host insects of the species of *Lysiphlebus* and *Aphelinus* that are known to also attack *Toxoptera*. This shows the varied host sources from which parasites may come in case of a serious invasion of *Toxoptera*.



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